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CONTENTS.

SUSAN HODGES

Gall Midges (Diptera-Cecidomyiidae) and their Parasites
(Hymenoptera) Living in Female Birch Catkins

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PART IX

GALL MIDGES (DIPTERA-CECIDOMYIIDAE) AND THEIR PARASITES (HYMENOPTERA) LIVING IN FEMALE BIRCH CATKINS

By SUSAN HODGES

(Department of Botany, The University Museum, Manchester)

I. INTRODUCTION

Larvae of three species of Cecidomyiidae were found living in the female catkins of birch trees in an area of Lindow Common, Wilmslow, Cheshire. Although these three species occupy the same general habitat, they have different feeding habits. The larvae of *Semudobia betulae* Winnertz are phytophagous, those of *Clinodiplosis* are inquilines feeding on fruits galled by *Semudobia betulae* and those of *Lestodiplosis* are predatory feeding mainly on *Clinodiplosis* larvae.

Such associations, in the same habitat, of several genera of Cecidomyiidae, have previously been recorded by Otter (1938), who found a complex of species of the genera *Lestodiplosis*, *Clinodiplosis* and *Dasyneura* in the flower heads of knapweed (*Centaurea*). Barnes (1948) found larvae of *Clinodiplosis piscicola* Barnes in pea pods infested with *Contarinia pisa* (Winnertz); he also states that the larvae of *Lestodiplosis* species are quite frequently found amongst the flowers and seeds of ornamental plants, together with *Clinodiplosis* larvae. Milne (1960) recorded ten species belonging to nine genera of Cecidomyiidae in clover heads. Parnell (1963) describes larvae of *Contarinia pulchripes* (Kieffer), *Clinodiplosis sarothamni* (Kieffer) and a *Lestodiplosis* species all inhabiting the cavities of broom pods (*Sarothamnus scoparius* L.).

The immature stages of Cecidomyiidae are often attacked by hymenopterous parasites, especially of the superfamilies Chalcidoidea and Proctotrupoidea. In Europe *Semudobia betulae* is recorded as being parasitised by *Platygaster* species (Proctotrupoidea; Platygasteridae), *Lioterphus pallidicornis* (Boheman) and *L. fuscicornis* (Walker) (Chalcidoidea: Torymidae), *Tetrastichus clavicornis* (Zetterstedt), *T. pallipes* (Dalman) and *T. escherichi* Szélenyi (Chalcidoidea: Eulophidae), *Pylonotus adamas* Walker and *P. achaeus* Walker (Chalcidoidea: Pteromalidae). The species found in the course of this study on Lindow Common were *Platygaster* species, *Lioterphus pallidicornis*, *Tetrastichus clavicornis*, and *Tetrastichus pallipes*. Felt (1915) states that several species of parasites have been reared from American material of

Semudobia betulae, but these are different from the European parasites.

Most of the work described here was carried out along the northerly and north-easterly edges of Lindow Common, Wilmslow, Cheshire (Grid Ref. SJ 834 816), between 1964 and 1966.

Both of the common British species of birch, *Betula verrucosa* Ehrhart and *B. pubescens* Ehrhart, were found to be infested by *Semudobia betulae*. Rostrup (1897) also records infestation of these two species, together with *Betula odorata* Reichenbach.

II. THE MORPHOLOGY AND BIOLOGY OF THE GALL MIDGES (DIPTERA: CECIDOMYIIDAE)

1. *Semudobia betulae* Winnertz

(a) Review of literature

The first description of adult *Semudobia betulae* was given by Winnertz (1853), who placed it in the genus *Cecidomyia*. Subsequent redescrptions were by F. Loew (1878), Theobald (1892), and Felt (1908). Kaltenbach (1874) described larvae supposed to be of this species but the larvae described are not those of *Semudobia betulae*. F. Loew (1878) first stated that the midge was a gall-maker. Rubsaamen (1891) placed the species in the genus *Hormomyia*. Kieffer (1898) originally placed *Semudobia betulae* in the genus *Oligotrophus*, but later, in 1913, he made it the type-species of his newly erected genus *Semudobia*.

(b) Morphology of the immature stages

The Egg

The egg (Fig. 8) is oval in shape, light orange in colour and measures 0.25 mm. in length. The chorion is smooth.

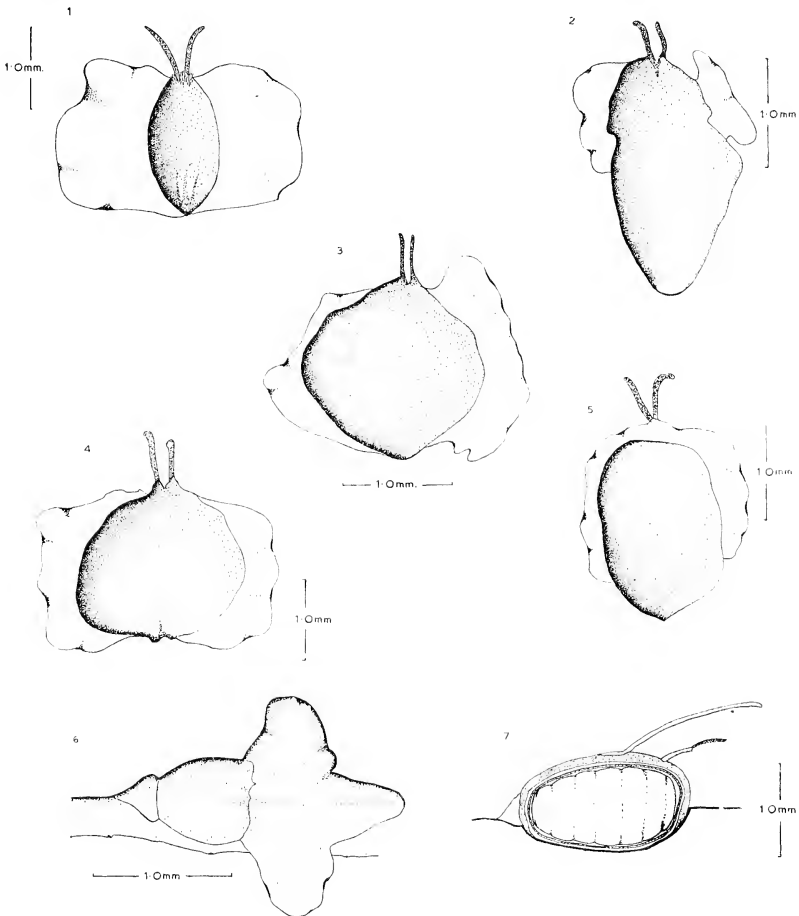
The Gall

Galling of the female birch catkin is caused only by *Semudobia betulae*. An infested catkin is discovered when the nuts are separated from the scale leaves. Each galled fruit is swollen, and the seed inside destroyed. Swelling in some fruits (Fig. 2) is accompanied by a corresponding reduction in wing size, while in others, the fruit (Figs 6 and 7) is swollen, but the wings are completely lost. In the latter, part of the axis of the catkin and the scale leaf are incorporated into the formation of the galled fruit; at maturity the wings and the scale leaf fall away. However, there are variations between these two extremes (Figs. 3 and 4). Prior to the pupation of the *Semudobia* larvae a characteristic window-like spot appears in each swollen nut (Fig. 5).

The First Instar Larva

The first instar larva, which consists of thirteen visible segments following the head, measures 0.2 mm. in length and is pale

orange in colour. The larva is without setae, and there is no sternal spatula or eye spot present (Fig. 9).



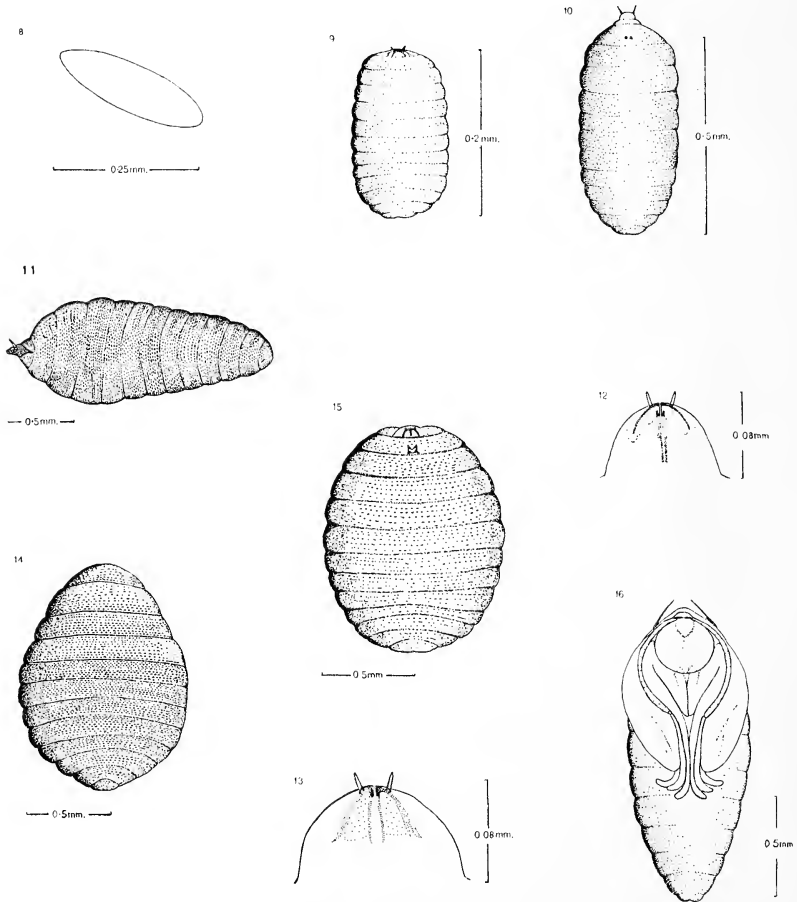
FIGURES 1-7, Birch (*Betula*) Fruits.—1, uninfected fruit; 2, infected fruit showing window-pit, and point of attachment to female catkin; 3-4, stages and variations of infection; 5, galled fruit showing window-pit; 6, exterior view of galled fruit destined to lose scale leaf and wings; 7, cross section of 6, showing dorsal view of larva inside.

The Second Instar Larva

The second instar larva measures 0.5 mm. in length and is pale orange in colour. The body lacks setae, but papillae start to develop at this stage. Growth of the sternal spatula commences, the tips of which develop first. Growth of the tips extends backwards as the larva develops (Fig. 10).

The Fully-grown Larva

The fully-grown larva (Fig 11) (when straightened under a cover slip) has a length of 2.0-2.5 mm. and a maximum width of 0.9-1.2 mm. The body is bright orange in colour and the surface papillate, but there are no setae. Each larva has thirteen visible segments following the head; a supernumerary segment, three thoracic segments and nine abdominal segments. The last twelve segments may be referred to as the body segments.



FIGURES 8-16, *Semudobia betulae* Winnertz.—8, egg; 9, first instar larva; 10, second instar larva; 11-15, adult larva; 11, side view; 12, ventral view of head; 13, dorsal view of head; 14, dorsal view of body; 15, ventral view of body showing sternal spatula; 16, ventral view of pupa.

The head (Fig. 12) measures 0.08 mm. in length. The outer edges of the head capsule are lightly sclerotised, and normally the whole structure is retracted into the supernumerary segment. Even though a magnification of $\times 100$ is used, the only clear detail of the head that can be seen is a pair of antennae which arise from the dorsal side of the head capsule (Fig. 13). Each antenna is composed of two segments, a short lower basal segment and a longer upper segment, the extremity of which is pointed. No eyes are present.

The supernumerary segment bears no appendages.

Dorsally, each body segment bears two types of papillae. Towards the anterior edge of each segment the papillae tend to unite to form striae while towards the posterior edge, the papillae are isolated and more rounded (Fig. 14). Respiration in all larvae of Cecidomyiidae is peripneustic (Kieffer 1900), and there are nine pairs of spiracular openings situated on body segments three, and segments six to thirteen inclusive. The larvae of *Semudobia betulae* are densely packed with a bright orange fat body, and no spiracular openings could be seen. The anal or ninth abdominal segment is bilobed.

Ventrally (Fig. 15) the papillae unite to form transverse striae again, while laterally they are isolated and more rounded. On the ventral surface of the prothorax lies the bifid sternal spatula, the length of which is 0.092 mm. The two lobes of the sternal spatula end in pointed tips which are heavily sclerotised.

The Pupa

The pupa (Fig. 16) measures 1.5 mm in length, being stout and narrowly oval in cross section. The cephalic horns are quite distinct. The thorax is yellowish orange in colour, and the wing pads fuscous, the colour darkening as the time of emergence approaches. The leg cases are dark yellowish brown and the abdomen dull orange-brown in colour. The abdomen is narrowly rounded apically.

(c) Life history

Semudobia betulae is one of the few gall midges to have been recorded from both the palearctic and nearctic, and probably occurs throughout Europe. In England, Bagnall and Harrison (1918, 1932) and Barnes (1925) have recorded the species from several counties. The author has records of *Semudobia betulae* from Lincolnshire, Cheshire, Kent, and Leicestershire. In fact, it is probably to be found wherever *Betula* grows.

F. Loew (1878) gave the first details concerning the life history of *Semudobia betulae* stating that the larvae are bright red in colour and usually live solitarily inside the seed capsule of the fruits of birch. When fully-grown in the autumn, the larva makes a transparent window-like spot on one side towards the top of the capsule. Pupation occurs just before emergence of the midges which takes place in March, April and May (Barnes 1951). Barnes

found that during 1925, in Kent, midges started emerging on April 7 and continued until April 20. In 1926 emergence took place between March 25 and April 10. Wahlgren (1944) recorded emergence between March 21 and 31 in 1941, when out of sixty specimens forty-one were females.

The author has found that the date of emergence is variable and depends upon prevailing conditions. The position of an area, the temperature, and consequently the stage of development of the birch trees are probably the most important determining factors concerning emergence. For example, adult gall midges emerged from fruits collected in Kent, in the middle of April, two weeks before they started to emerge from fruits collected in Cheshire. In the same year (1966), the unfolding of the birch leaves in Kent was two weeks ahead of their appearance in the north.

When fruits were brought into a warm room, emergence of *Semudobia betulae* occurred at the end of February, whereas at the site where they were collected, emergence occurred during the last week in April. In the field, *Semudobia betulae* adults emerged a few days after pollination in *Betula*. In all cases, the period of emergence of the adult covered approximately two to three weeks.

On Lindow Common, in 1965 and 1966 emergence of the adult insects in the field began in the last week of April (Fig. 46). Mating occurs and eggs are laid about the first week in May. The females were seen to be most active one hot, sunny afternoon (2nd May 1966), when practically every female birch catkin was being attacked by a female *Semudobia*. At this stage, the female catkins are pointing in an upward direction. The female insect flies to a catkin and always first walks to the base of that catkin. During these operations, the antennae are arched, the tips wavering above the catkin but never touching the fruits. One third of the way up the catkin from the base, the female midge starts to oviposit between the fruits and the scale leaves. During oviposition the female arches her abdomen, and then pokes the tip of the ovipositor between the parts of the female catkin. One egg is laid at each insertion of the ovipositor between the scale leaves. When the female reaches the tip of the catkin she turns round and proceeds to the basal region. Oviposition begins again, a little further round the circumference of the catkin, but still in the same upward direction. Often two females are seen ovipositing on one catkin. A female will sometimes rest half way up a catkin, stopping and straightening her ovipositor.

The first instar larva emerges from the egg within three to five days of being laid between the scale leaves. At the end of the second week in May, first instar larvae are found moving sluggishly between the fruits and scale leaves. Each larva penetrates a fruit wall and enters the seed. The tissue of the fruit wall is so soft, that no mark is left by the gall-making larvae. The first instar larva is capable of wriggling movements inside the gall. Usually only one larva is found in one seed in a fruit cavity, but occasionally (in about 5% of galls) two larvae are found.

An early second instar larva is found inside the copious galled tissue of the seed by the middle of June. The second instar is a rapidly feeding stage, with the gall tissue disappearing quickly.

The fully-grown larva is found in August and September. All the copious galled tissue has been eaten and the larva lies in, and completely fills, the enlarged cavity of the fruit (Fig. 7). There is no sign of excrement inside the gall. The larva is inactive.

The most prominent organ of the fully-grown larva is the sternal spatula, but the function of this organ is open to question. As the spatula develops at the end of the feeding phase, a post-feeding function seems probable.

There is no reference in the literature to the function of the sternal spatula of *Semudobia betulae*. Pitcher (1957) states that of the possible post-feeding functions, the preparation of a pre-emergence hole for an imago, which would otherwise be entombed in a hard gall, seems the most probable answer. This theory has the support of many observers. Kieffer (1894, 1900), has claimed that the best developed and the most heavily chitinised spatulae are to be found in those species in very hard galls. Therefore in *Semudobia betulae* the function of the sternal spatula is most probably to prepare a pre-emergence hole for the imago in the woody fruit. When fully-grown in the late summer, and prior to cocoon formation, the larva makes a window-like spot on one side towards the top of the fruit.

The cocoon is apparently formed by a secretion produced over the whole surface of the fully-grown larva. Cocoon formation occurs at the end of June or the beginning of July.

The food web in the gall of *S. betulae* is illustrated in Fig. 50.

2. *Clinodiplosis* species

(a) Problems of identification

There is no mention in the literature of a *Clinodiplosis* species associated with female birch catkins. The species belonging to this genus are difficult to separate morphologically and until a detailed and extensive revision of this genus is undertaken, including both morphological and biological data, it is debatable whether or not the already described *Clinodiplosis* species are all valid, or whether some of the names are synonymous and there are only a few polyphagous species.

(b) Morphology of the immature stages

The First Instar Larva

The first instar larva (Fig. 17) consists of thirteen body segments following the head and measures 0.45 mm. in length and 0.25 mm. in width. The double eye spot on the dorsal side of the prothorax is the most prominent feature of the larva, together with the spiracles on the eighth abdominal segment.

The Second Instar Larva

The body of the second instar larva (Fig. 18) measures 1.0 mm. in length and 0.35 mm. in width at the widest point. The spiracles start to develop on the dorsal surface of the prothorax and the first to eighth abdominal segments dorsally. The prothorax also has a double eye spot dorsally. Respiration is peripneustic. Development of the sternal spatula commences at the chitinised tips.

The Fully-grown Larva

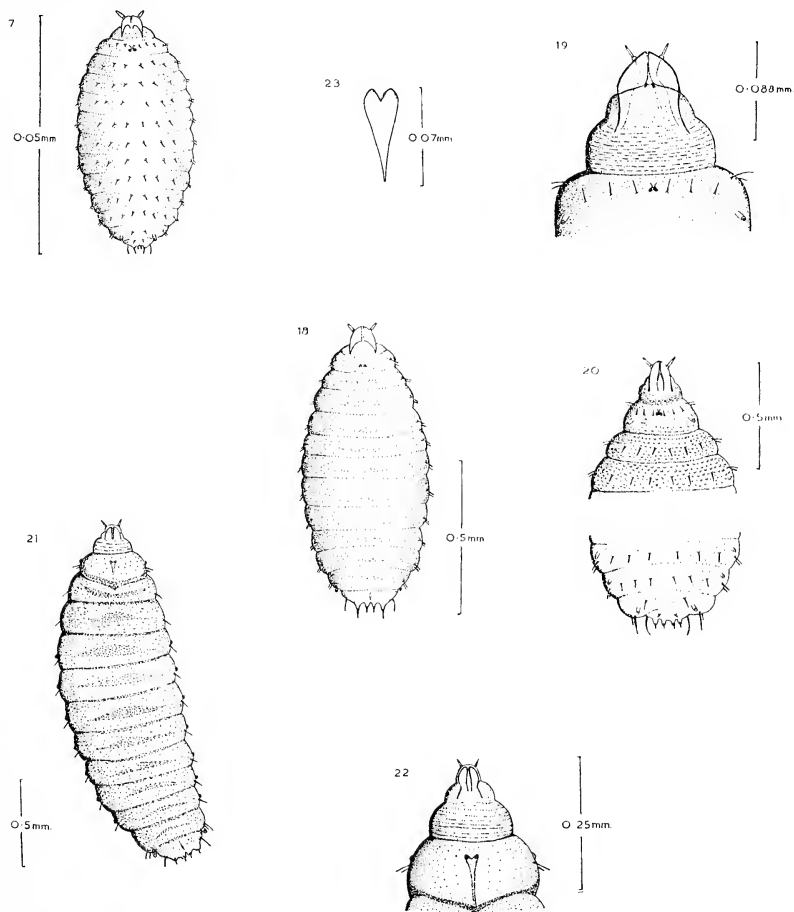
The fully-grown larva measures 1.5-2.2 mm. in length and 0.5-0.6 mm. in width at the widest point along the body. The body is bright orange in colour and the surface is papillate. It may be readily distinguished from the larva of *Semudobia* by the presence of setae on the body segments. The body is composed of thirteen body segments, after the head, including the supernumerary segment, as in *Semudobia*.

The length of the head (Fig. 19) to the tip of the horns is 0.088 mm. and the maximum width 0.056 mm. The outer edges are heavily sclerotised and localised thickenings can be seen on the head capsule. Although a magnification of $\times 100$ is used the only distinct structures are the two antennae. These arise from the dorsal side of the head. Each antenna measures 0.016 mm. in length and is composed of two segments, a short lower basal segment and a longer upper segment, the extremity of which is pointed. No eyes are present on the head capsule.

Normally the head capsule is retracted into the supernumerary segment. The latter measures 0.08 mm. in length and bears no appendages.

Dorsally, each body segment bears evenly distributed, rounded papillae (Fig. 20). Ventrally, the thoracic and abdominal segments have regions of more densely crowded papillae (Fig. 21). The setal pattern of the body segments except the last two and the supernumerary segment, consist of three pairs of dorsal setae and two pairs of lateral setae. The eighth abdominal segment has a dorsal pair of setae between the spiracles and two lateral pairs of setae. The last abdominal segment has two pairs of very short terminal, blunt, thick setae on tubercles. Immediately above, and slightly anterior to the lateral pair is a small pair of dorsal setae, while laterally, and immediately below is situated a pair of long postero-lateral setae. The latter are the longest setae on the body. The ninth abdominal segment also has a ventral anus. The ventral surface of the prothorax (Fig. 22) bears a well-developed bilobed sternal spatula, the tips of which are sclerotised. The stem of the spatula (Fig. 23) is apparent only in the fully-grown larva, the full length being 0.7 mm. The respiratory system is peripneustic, there being nine pairs of dorsally situated spiracles on the prothorax and each of the first

eight abdominal segments. A double eye spot, which is 0.04 mm. long is present dorsally on the prothorax. The eye spot is dark red to black in colour, and consists of two half-moon shaped pieces which touch at the base. The function of this structure is probably photosensory.



FIGURES 17-23, *Clinodiplosis* species.—17, first instar larva; 18, second instar larva; 19-22, full grown larva; 19, dorsal view of head, supernumerary segment and prothorax; 20, dorsal view of body; 21, ventral view of body; 22, ventral view of head and anterior segments of body to show sternal spatula; 23, sternal spatula.

(c) Life history

Inquilinism is frequent among *Clinodiplosis* species (Kieffer 1898, 1900), although some are freely phytophagous, not associated with a gall-forming species (Milne 1960).

The adult flies of the *Clinodiplosis* species found in the present study emerge during the last two weeks in June and the first week in July. Oviposition begins the last week in June.

Only female catkins containing fruits galled with *Semudobia betulae* are infected with *Clinodiplosis*. The eggs are laid one by one, often as many as twelve being placed in the same area of the catkin. Several females may lay eggs on the same catkin. As many as twenty-nine larvae of different instars were counted on one catkin at the end of July 1965.

First instar larvae were most common between the fruits in the first week of July, second instar in the second week and third instar the third week in 1965. The larvae are quite active compared to those of *Semudobia betulae*, moving between the fruits with the aid of the sternal spatula. *Clinodiplosis* feeds on more than one gall of *Semudobia betulae*, the host being destroyed.

When fully-grown, in the autumn, the third instar larvae fall to the ground, or are dispersed by wind with the fruits of female catkins. Each larva burrows into the soil, presumably with the aid of the sternal spatula, and over-winters in the prepupal stage without forming a cocoon. Pupation occurs prior to emergence in late spring of the following year.

3. *Lestodiplosis* species

(a) Problems of identification

Bouché (1834) and Perris (1870) were the first two authors to describe the pseudopods typical of the genus *Lestodiplosis*.

There is no mention in the literature of a *Lestodiplosis* species associated with female birch catkins. However, an unidentified *Lestodiplosis* species was recorded by Felt (1918) in America as being obtained from under decaying bark of birch, and stated to be probably predaceous.

As with the genus *Clinodiplosis*, the species belonging to the genus *Lestodiplosis* are difficult to separate morphologically, and the entire genus is badly in need of revision. Until this is carried out it will remain unknown whether or not there are only one or two polyphagous species, or a larger number of oligophagous and monophagous species.

(b) Morphology of the immature stages

The Fully-grown Larva

The fully-grown larva (Fig. 24) measures 2.2-2.8 mm. in length and 0.4-0.7 mm. in width, at the widest point along the body. The colour of the body is bright orange, and the surface crenulated and provided with long setae. The body is composed of a head, supernumerary segment, three thoracic segments and nine abdominal segments. A characteristic feature of the larva of *Lestodiplosis* is the pseudopods.

The length of the head (Fig. 25) from the tips of the antennae to the tips of the horns measures 0.13 mm. and the width at the widest point, 0.056 mm. The head capsule consists of an elongated and ill-defined, chitinous cone of varying thickness. Laterally, the base of the cone is produced posteriorly into two strongly chitinised horns. Under a magnification of $\times 100$, details of the head capsule are obscure, except for the antennae and the presumed mandibles.

The antennae are two-jointed and are borne on lateral outgrowths from the head. The lower basal joint is short and closely connected to the head capsule, while the terminal joint is longer and finely pointed. The presumed mandibles are laterally placed, and hook-like. They have wide triangular bases which appear to articulate with the head capsule. The mandibles are set at an angle to each other in the cone, with their bases wide apart, but their convex sides touching each other in the middle. They can protrude dorsally at the apex of the head-cone. Because of their sickle-like shape their points spread out laterally the more their convex sides come into contact with each other.

The oesophagus is a thickly chitinised tube, which is seen to pass back from the head capsule near to the ends of the backwardly projecting horns, where it joins the fore-gut. No eyes are present on the head capsule.

The supernumerary segment measures 0.036 mm. in length and bears no appendages. Normally the head is retracted into the supernumerary segment.

Dorsally the prothorax (Fig. 26) bears three pairs of setae which form a transverse row on either side of the mid-dorsal line. The middle pair is slightly shorter than the other and set rather more towards the posterior of the segment. There is a double eye spot on the mid-dorsal line between the setae. However, in *Lestodiplosis*, the sternal spatula is absent. Laterally, there are two setae of equal length on each side, one above the other, and situated anteriorly to the prothoracic spiracles. This setal pattern is common to all the body segments except the eighth and ninth abdominal segments.

Ventrally, there are three pairs of setae on the prothorax, three setae on each side of the mid-ventral line (Fig. 27). The most lateral pair of these setae is the same length as the dorsal setae, and is set to the anterior of the segment: the middle pair is small, while the inner pair is a little longer than the middle pair, and is set posteriorly. On the meso- and meta-thoracic segments the three pairs of ventral setae are arranged around the posterior base of the ventral projection from which the pseudopods arise. On the first seven abdominal segments, the middle and inner pairs of central setae are absent, while the outer pair remain in the same position as on the thoracic segments. The meso- and meta-thoracic segments each bear two pseudopods, while the first

seven abdominal segments each have three on the ventral surface. The projection from which the pseudopods arise is surrounded by rows of short pointed papillae (Figs. 27 and 28).

Laterally the more dorsal seta is situated just below the spiracles, while the dorsal setae are all arranged in a straight line transversely across the centre of the segment. The eighth abdominal segment has two dorsal setae only. These are situated between the two spiracles, and slightly towards the posterior of the segment. There are no ventral setae. Around the end of the ninth abdominal segment there is a transverse row of four long and curved setae, and a little dorsal to these a pair of longer setae situated between the outer and inner setae of the row below. These three setae are set on pronounced papillae. Between the two dorsal setae on the last abdominal segment lies the dorsal anus — a characteristic of the genus *Lestodiplosis*. There are three small swellings on the ventral surface of the ninth abdominal segment (Fig. 28).

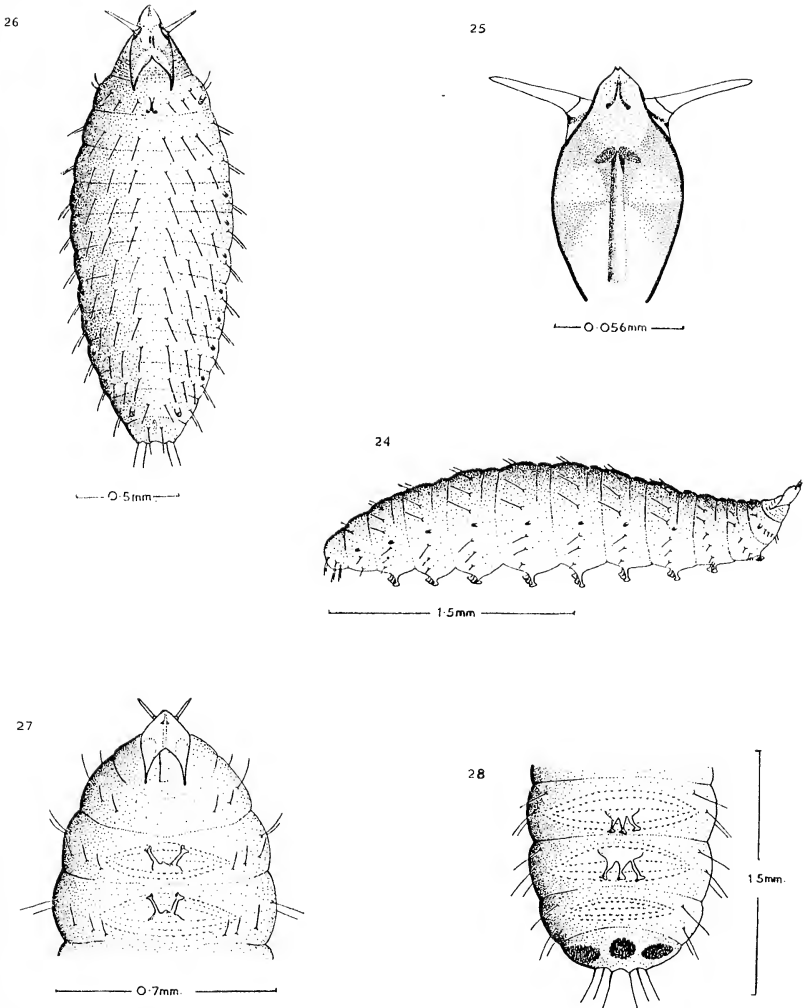
(c) Life history

It would appear that typically *Lestodiplosis* larvae are predatory as recorded by Felt (1918) and Otter (1934). The larvae often use other Cecidomyiid larvae as prey, as recorded by Barnes (1928), Otter (1938), Milne (1960) and Parnell (1963).

The adults of the species of *Lestodiplosis* under review here, emerge from the end of June to the middle of July, the emergence extending over approximately two weeks. Oviposition occurs from the beginning of the first week in July. The female midges walk over the female catkins with antennae raised. One or two eggs are laid on each catkin, each being laid between the scale leaves. Sometimes an egg of *Lestodiplosis* is deposited on a catkin containing only *Semudobia* larvae and hymenopterous parasites, but usually *Clinodiplosis* is present in the catkin selected for oviposition by *Lestodiplosis*.

The first instar larva is capable of rapid movement between the fruits and scale leaves, and is most common during the second week in July. The second instar is predatory on all instars of *Clinodiplosis* larvae and is most common in the third week. The third instar is less active than the previous two instars and is most prevalent during the fourth week in July. However, all the stages of *Lestodiplosis* larvae are more active than those of *Clinodiplosis*. If *Clinodiplosis* is absent, *Lestodiplosis* presumably will feed on *Semudobia* and the hymenopterous parasites.

When fully-grown in the autumn the third instar larvae fall to the ground or are dispersed by wind with the fruits or female catkins. They burrow in the soil with the end of the pseudopods and overwinter in the prepupal phase without forming cocoons. Pupation occurs in the late spring.



FIGURES 24-28, *Lestodiplosis* species.—24-28, full grown larva; 24, side view showing pseudopods, spiracles, and setal pattern; 25, dorsal view of head showing antennae, mandibles and oesophagus; 26, dorsal view of body; 27, ventral view of head and anterior segments of the body; 28, ventral view of the last abdominal segments of the body.

III. THE MORPHOLOGY AND BIOLOGY OF THE PARASITES (HYMENOPTERA)

1. *Platygaster* species (Proctotrupoidea: Platygasteridae)

(a) Problem of identification

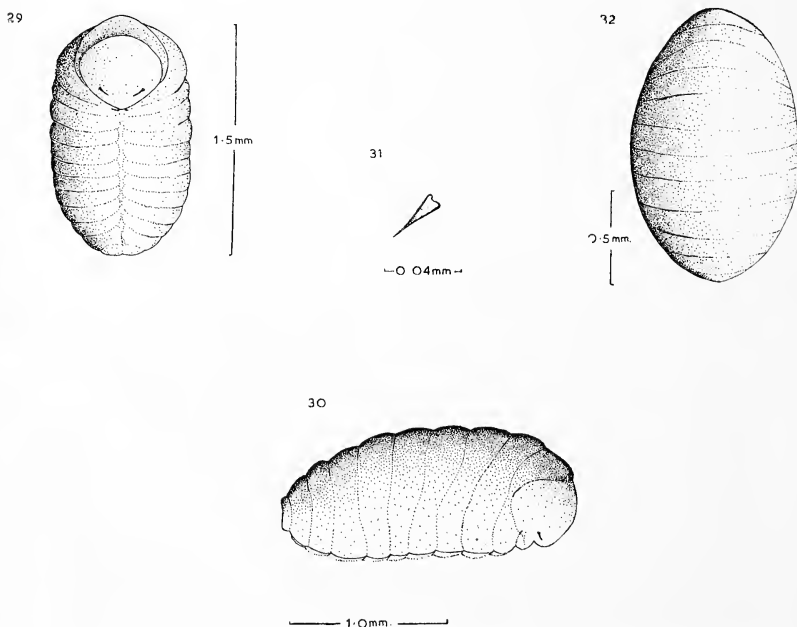
Kieffer (1916) recorded *Platygaster betularia* Kieffer as a European parasite of *Semudobia betulae*. It is very probable that this is the same as the species at present under consideration.

The early instar larvae are very fragile, and they disintegrate readily on removal from the host.

(b) Morphology of the immature stages

The Fully-grown Larva

The fully-grown larva (Figs. 29 and 30) is white in colour and soft to the touch. Disintegration occurs soon after removal from the cocoon. The length of the body is 1.0-2.0 mm. and the width at the widest point 0.8-1.0 mm. The body of the larva is oval in shape and distinctly segmented into a head and eleven body segments. The surface is smooth, as there are no spines or fleshy processes present. The mandibles (Fig. 31) are 0.04 mm. in length, finely pointed and widely spaced.



FIGURES 29-32, *Platygaster* species.—29, ventral view of mature larva; 30, side view of mature larva; 31, mandible; 32, dorsal view of cocoon.

The Cocoon

The larval skin of the parasitised *Semudobia betulae* forms the cocoon for *Platygaster* (Fig. 32). The remains of the mouth parts and the sternal spatula of the third instar of *Semudobia betulae* are seen on the vertical side of the "cocoon".

The Pupa

The pupa is stout and narrowly oval in shape. The body measures 1.3 mm. in length and is very fragile. The colour is white except for the compound eyes which are bright red at the end of the period of pupation. Development of the eye pigment is gradual, being white at the beginning of pupation and passing gradually to bright red at the end.

(c) Life history

Oviposition in the egg of the host, followed by development and emergence, was first observed in *Platygaster* by Herrick (1841) working with *Platygaster hiemalis* Forbes. The actual manner of oviposition and development was not substantiated until the publication of Marchal's work between 1896 and 1906 on the biology of several species of *Platygasteridae*.

The adults of the species of *Platygaster* studied here emerge simultaneously with their host, *Semudobia betulae*, in the last week in April and the first week or ten days in May (Fig. 47). The insects are very active. During courtship, a male flies to a female, mounting her back and drumming on her head with his antennae. Copulation sometimes follows, the period of which lasts for a maximum of sixty seconds. If several males are together this same procedure of mounting one another occurs.

An egg is laid inside the egg of *Semudobia betulae* which lies between the scale leaves and fruits of the female catkins. The egg of the parasite enters the seed cavity while inside the first instar larva of the host. The egg of *Platygaster* lies inside the haemocoel of the larva of *Semudobia*.

The mature larva is inactive and lies in the larval skin of the host which forms a "cocoon". The remains of the head and sternal spatula of a *Semudobia* larva that has been parasitised can be seen on the ventral surface of the "cocoon".

Larval development and pupation is completed by the end of August, and *Platygaster* spends the winter as an adult enclosed within the cocoon and fruit cavity. Development here is monembryonic, that is, one adult only develops from each egg. Some species of *Platygaster* are polyembryonic. There is only one generation a year.

2. *Lioterphus pallidicornis* (Boheman) (Chalcidoidea: Torymidae)

(a) Review of literature

Lintner (1888) recorded rearing a *Torymus* species from English galled seeds sent to him by Peter Inehbald. Felt (1915), Hoff-

meyer and others recorded *Lioterphus (Torymus) pallidicornis* as a European parasite of *Semudobia betulae*.

(b) Morphology of the immature stages

The Egg

The egg measures 0.35 mm. in length. The chorion is smooth and unpigmented. The body of the egg is cylindrical, with a small nipple-like projection at one end.

The First Instar Larva

The first instar larva (Figs. 33, 35 and 36) consists of a head and thirteen body segments. The length of the body is 0.4 mm. and the colour is white. The head bears a pair of brown, pointed mandibles. Each body segment except the last has a pair of dorsal setae, which approximate to the size of the head in length, and are the longest setae on the body. The first twelve body segments have a pair of lateral setae, shorter than the dorsal setae, and three shorter pairs of dorsal setae. The last segment is bilobed posteriorly.

The Fully-grown Larva

The colour of the fully-grown larva (Fig. 37) varies from white to pale cream, and is due to the closely packed fat body that shows through the integument. The gut is seen through the body wall as a grey area. The body measures 2.0 mm. in length and 0.7 mm. in width at the widest point. Each segment after the head bears a pair of longer setae at the mid-dorsal line. Body segments one to twelve have a pair of lateral setae, a shorter pair of ventral setae, a pair of dorso-lateral setae and a pair of ventro-lateral setae. There are nine pairs of spiracles on segments two to ten, each pair being situated towards the anterior border of its segment.

In front view the head (Fig. 38) of the adult larva is pear-shaped and measures 0.4 mm. in length. The most prominent structures are the simple, pointed mandibles (Fig. 39), with a length of 0.05 mm., and the double-pointed sclerotised "snout" (Fig. 40) which lies above them and measures 0.02 mm. The projection is comparable in position to the raised area in *Torymus nigricornis* Boheman recorded by Askew (1965). Other chalcid larvae with facial teeth are those of species of *Stenomalina* and *Chlorocytus* (Graham and Claridge 1965), both of the family Pteromalidae. No other Torymids are known to have these teeth, though the larvae of *Oligosthenus stigma* (Blair 1945) and *Megastigmus dorsalis* (Fabricius) (Askew 1966) have sclerotised facial depressions. The function of these structures is unknown. The antennae are small and are situated near the outer borders of the raised areas of the frons. There are six pairs of long setae and two pairs of shorter setae on the head.

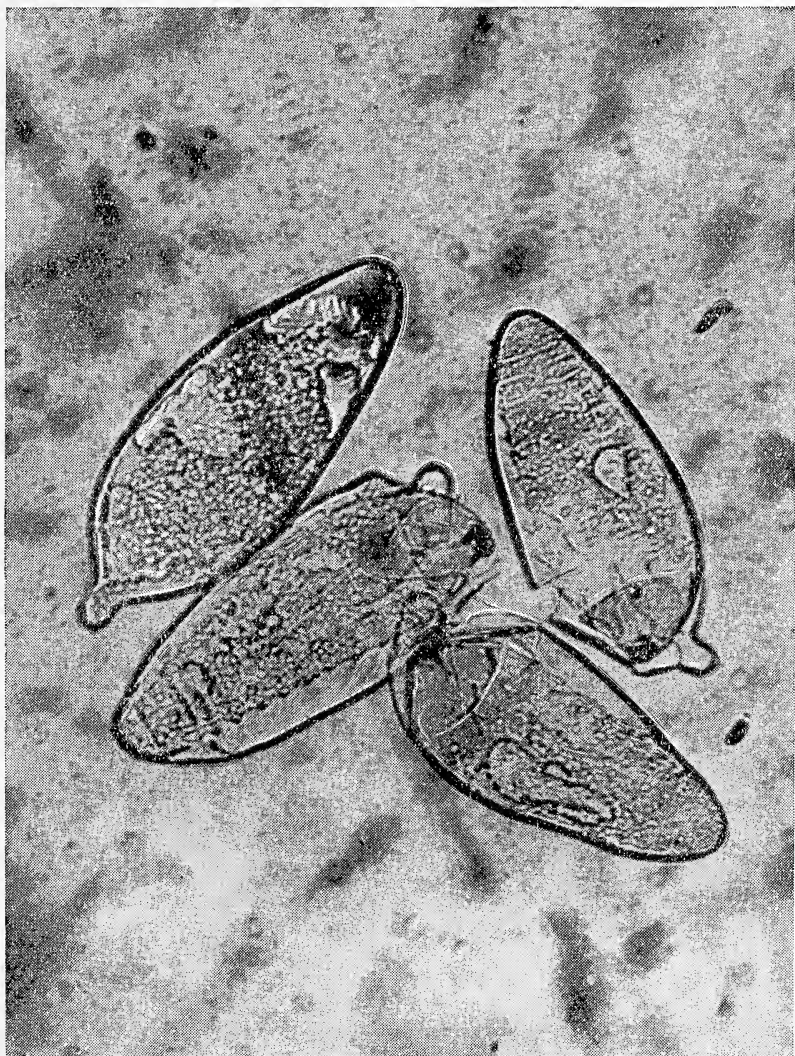
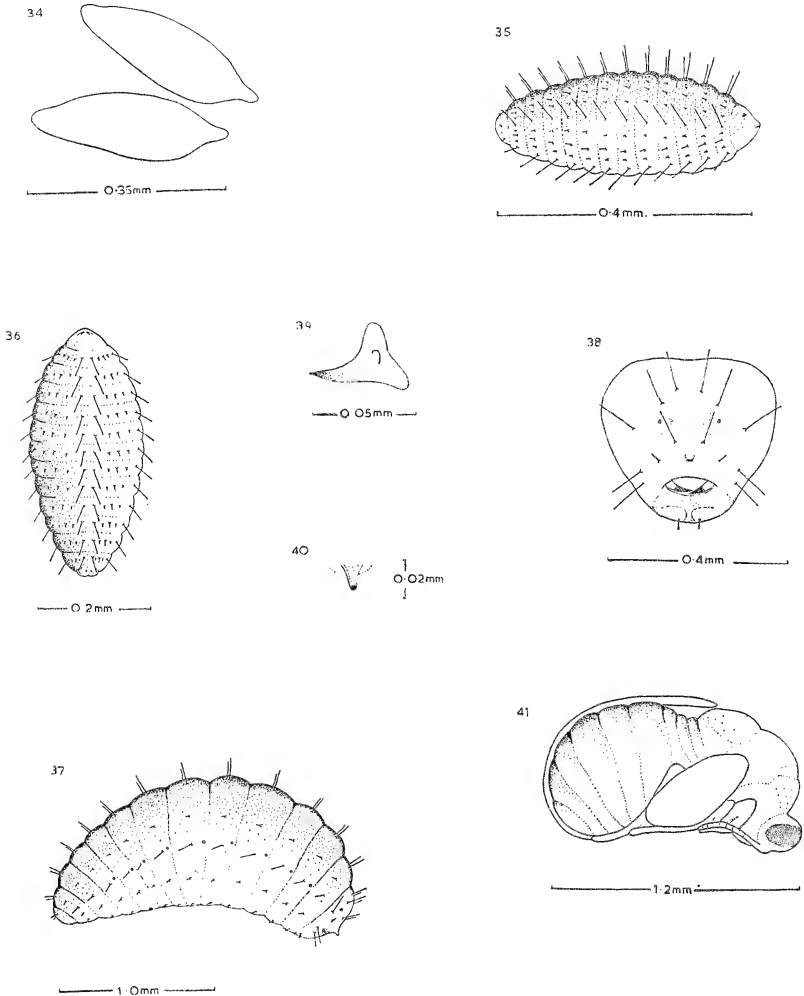


FIGURE 33, *Lioterphus pallidicornis* (Boheman).—33, first instar larvae emerging from egg cases.

The Pupa

The pupa of *Lioterphus pallidicornis* is bright yellow in colour, except for the bright orange eyes and ocelli, the most prominent features of the body. The female pupa (Fig. 41) has a long ovipositor curved back anteriorly in the mid-dorsal line. The pupa measures 1.2 mm. in length and 0.7 mm. in width. Prior to emergence, the green-black colour of the adult insect can be seen through the thin pupal integument.



FIGURES 34-41, *Lioterphus pallidicornis* (Boheman).—34, eggs; 35, side view of first instar larva; 36, dorsal view of first instar larva; 37-40, full grown larva; 37, side view; 38, face view of head; 39, mandible; 40, "snout"; 41, female pupa.

(c) Life history

Adults of *Lioterphus pallidicornis* emerge between the second week in June and the second week in July, the flight period lasting approximately five weeks (Fig. 48). Both the males and females are very active. Mating was observed one afternoon. The female in a walking position, was approached by the male and copulation occurred with the male clinging beneath the abdomen of the female, ventral side uppermost, legs and antennae arched and with the head pointing in the opposite direction to the head of the female. The female dragged the male along with her, for thirty seconds, while copulation occurred.

The adult female *Lioterphus* walks over the female birch catkin probing with her long ovipositor between the fruits. In one case, the posterior part of the abdomen, the stylets, and the long ovipositor of the female *Lioterphus* were found passing through three layers of fruit and scale tissue before ending in a galled seed containing a *Semudobia betulae* larva. The point of entry of the ovipositor in the fruit remained as a brown scar. *Lioterphus* eggs were usually found at the rate of two per fruit. Up to eight eggs have been found in a galled seed cavity containing a *Semudobia betulae* larva. This has probably arisen because several parasites have oviposited in the same fruit.

In each of three fruits dissected, there were two eggs of *Lioterphus pallidicornis* lying on top of a *Platygaster* cocoon. These eggs were found in December and had never developed. However, it seems probable that *Lioterphus* larvae will feed on *Semudobia* larvae which contain young stages of *Platygaster*.

Normally, of the two eggs laid inside the galled fruit containing a *Semudobia betulae* larva, only one develops. However, if there are two host larvae within the fruit, both parasite eggs develop.

The first instar larva of *Lioterphus pallidicornis* develops within five days and becomes attached to the middle body segments of *Semudobia betulae*. The parasite is attached to the dorsal surface of the host, by the last abdominal segment. The ectoparasitic larva is very active, and moves from side to side, pulling at the host with each movement.

In the majority of the fruits infected with *Lioterphus pallidicornis*, the contents of the fruit cavity include an egg, empty egg case, and first instar larva of *Lioterphus*, and a larva of the host, *Semudobia betulae*.

The well-developed mandibles of the second instar of the parasite are used for feeding on the host. The larva is very active, the "snout" being thrust back and forth, during movement of the whole body. Pupation occurs in the summer of the following year, prior to emergence of the adult insect.

From fruits collected in Kent in the spring of 1966, and brought into the laboratory, two species of *Lioterphus* emerged. These included twenty males of *L. pallidicornis*, with pale yellow antennae, and thirty-two males of *L. fuscicornis*, with dark brown antennae. There were thirty-five females, with light yellow

antennae, which presumably included both *L. pallidicornis* and *L. fuscicornis*, although no distinct difference was seen. *L. fuscicornis* was not discovered at Lindow Common.

3. *Tetrastichus clavicornis* (Zetterstedt) and *T. pallipes* (Dalman) (Eulophidae: Tetrastichinae)

(a) Review of literature

Lintner (1888) recorded rearing a *Tetrastichus* species from English galled seeds sent to him by Peter Inehbald. In the present study, two species of *Tetrastichus* have been found, *Tetrastichus clavicornis* (Zetterstedt) which is a frequent parasite of *Semudobia betulae*, and less commonly, *Tetrastichus pallipes* (Dalman). Graham (1960) has recorded *T. pallipes* investigating the galls of the Cecidomyiid *Iteomyia capreae* (Winnertz) on willow, *Salix caprea* L. *Tetrastichus escherichi* Szelényi has been recorded as a parasite of *Semudobia betulae* in Germany and Hungary by Domenichini (1965). However this species has not been found in this study.

(b) Morphology of the immature stages

The Fully-grown Larva

The fully-grown larva (Fig. 42) consists of a head and thirteen body segments. The length of the body is 1.5 mm. and the width 0.5 mm. at the widest point. The colour varies from cream to dark yellow. This larva is readily distinguished from that of *Lioterphus pallidicornis* by the absence of setae. Body segments two to ten have a pair of spiracles towards the anterior of each segment. The head (Fig. 43) measures 0.24 mm. in depth, the most prominent features being the two pointed mandibles (Fig. 44), each with a length of 0.05 mm., and a pair of short, squat, antennae.

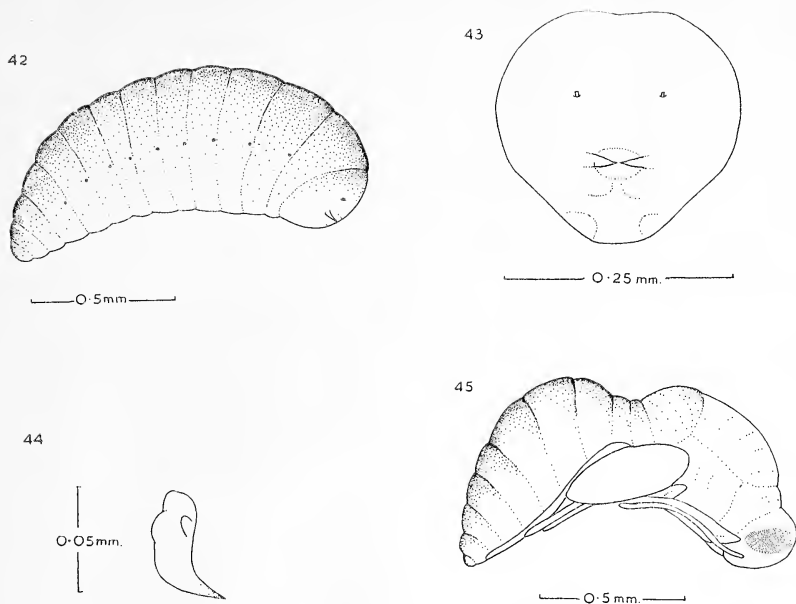
The Pupa

The pupa (Fig. 45) of *Tetrastichus clavicornis* measures from 1.5 mm. (male) to 2.5 mm. (female) in length and 0.5 mm.-0.8 mm. in width. The colour of the body is creamish-white at first, changing gradually to black, as the adult insect develops.

(c) Life history

The adults of *Tetrastichus clavicornis*, the dominant species of *Tetrastichus* parasitic on *Semudobia betulae*, are in flight the last week in May to the last week in July. *Tetrastichus pallipes*, an occasional parasite, emerges between the last week in May and the last week in June (Fig. 49). There is no evidence that either species has more than a single generation a year.

Prior to emergence, each adult cuts a small round hole in the window pit if present, or the thick fruit wall if not. The procedure is carried out by the mouth parts, the debris mostly falling to the



FIGURES 42-45, *Tetrastichus clavicornis* (Zetterstedt).—42-44, mature larva; 42, side view; 43, face view of head; 44, mandible; 45, male pupa

outside of the fruit. The head of the adult emerges first, when the antennae are projected forwards and investigate the area surrounding the achene. Next, the first pair of thoracic legs emerge, when the insect can grasp the wall of the fruit and the surrounding ones. Then the remaining two pairs of legs, followed by the rest of the body, are pulled clear of the fruit.

This process of emergence is variable in time: it can take as little as thirty minutes, or as long as twenty-four hours. For example, the emergence hole may be made one day, and the insect rest and emerge the following day. Occasionally an insect will only get half way out of the fruit and become trapped, and eventually die. On emergence, both males and females undergo a rapid cleaning process.

When the males and females first emerge, a male and female approach each other, waving their antennae for a few seconds. Approximately one hour later the males become very active and begin pursuing the females. A female will beat her wings as the male approaches. The male mounts the female's back and beats her on the head apparently with the swollen basal part of his antennae. The female becomes still and copulation occurs, lasting for a period of one to two minutes. The male flies away and undergoes a rapid cleaning process, while the female rests before resuming flight again.

Both species of *Tetrastichus* mentioned in this study are endoparasitic on *Semudobia betulae*. One egg is laid internally in each host larva. The larvae of *Tetrastichus* are very inactive in all their development stages. On dissection from a fruit, a fully-grown larva free of the remains of its host will only move when touched. The species overwinters as a fully-grown larva.

Presumably all sizes of host larva may be attacked by *Tetrastichus clavicornis*, and its extended flight period (Fig. 49) contrasts strongly with that of *Platygaster* (Fig. 47) which oviposits only in the egg stage of *Semudobia betulae* which is of short duration.

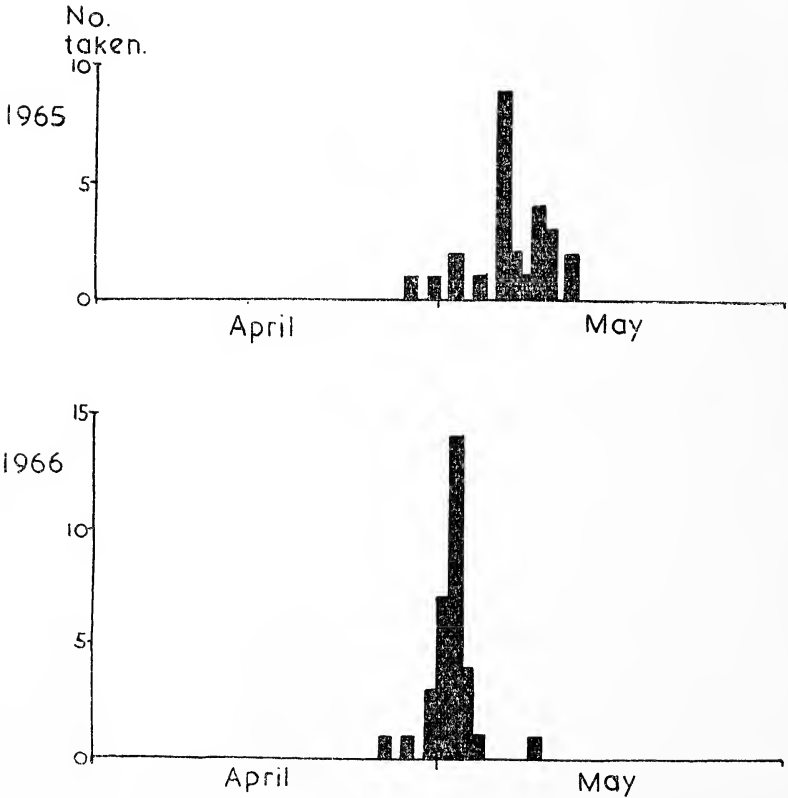


FIGURE 46.—The field captures of adult insects of *Semudobia betulae* on Lindow Common are shown for 1965 and 1966 respectively.

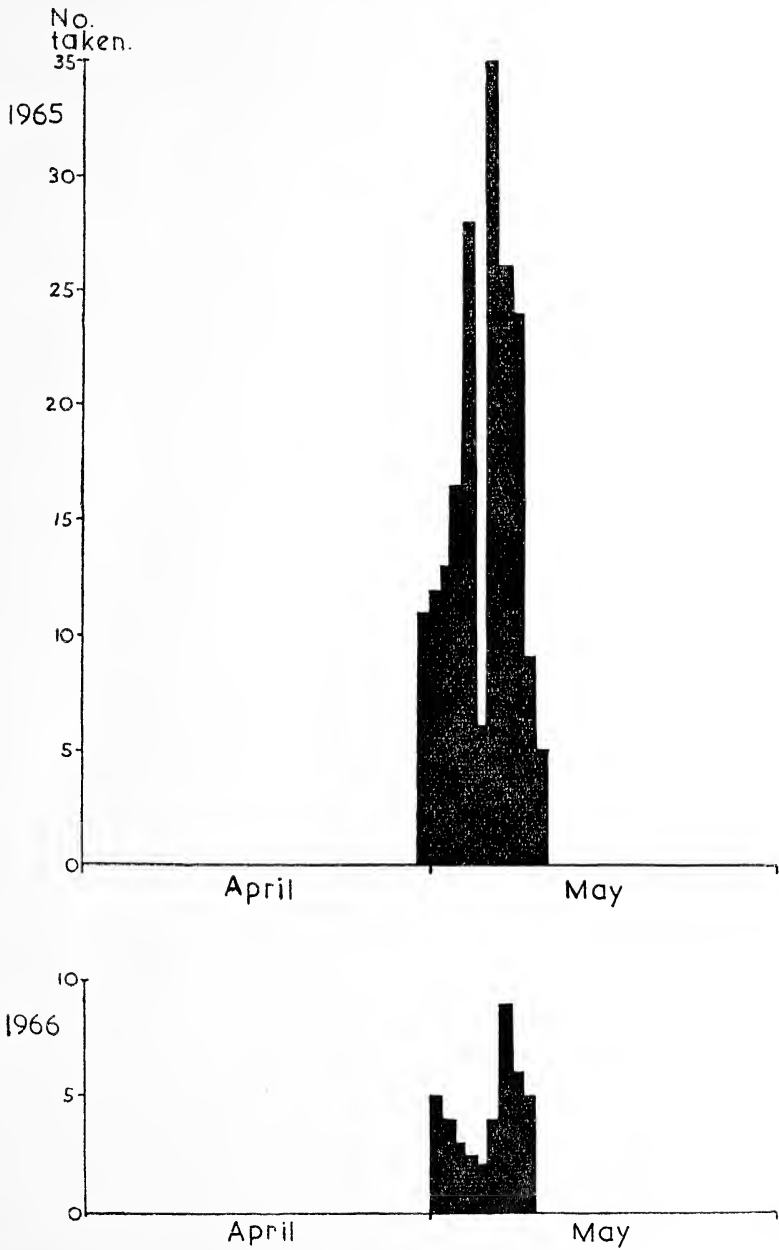


FIGURE 47.—The field captures of adult insects of *Platygaster* species on Lindow Common are shown for 1965 and 1966 respectively.

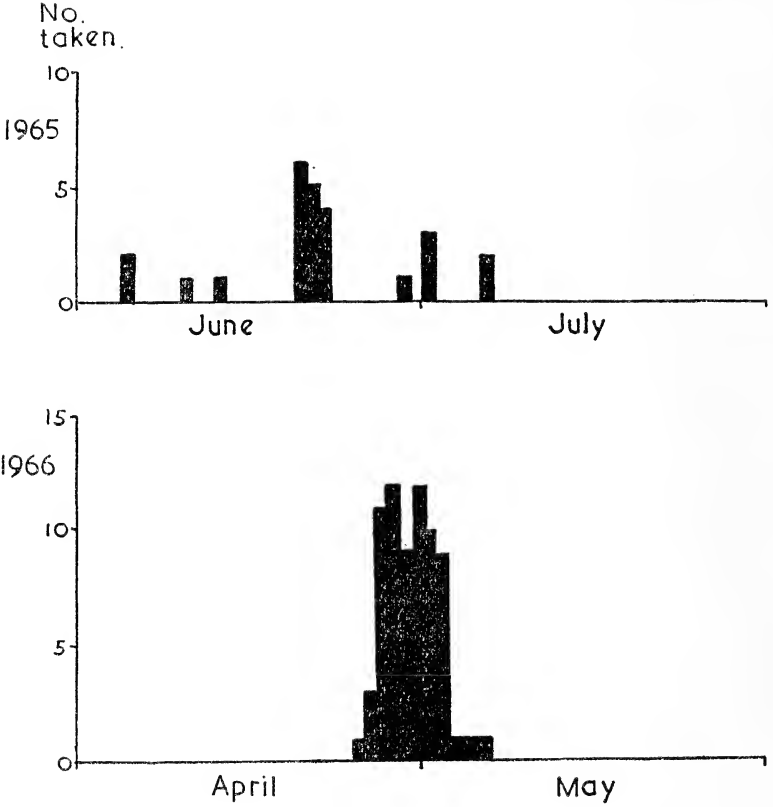


FIGURE 48.—The field captures of adults of *Lioterphus pallidicornis* on Lindow Common, are shown for 1965. The emergence of the adults of *L. pallidicornis* and *L. fuscicornis* are shown from fruits collected in Kent in the early spring and brought indoors in 1966.

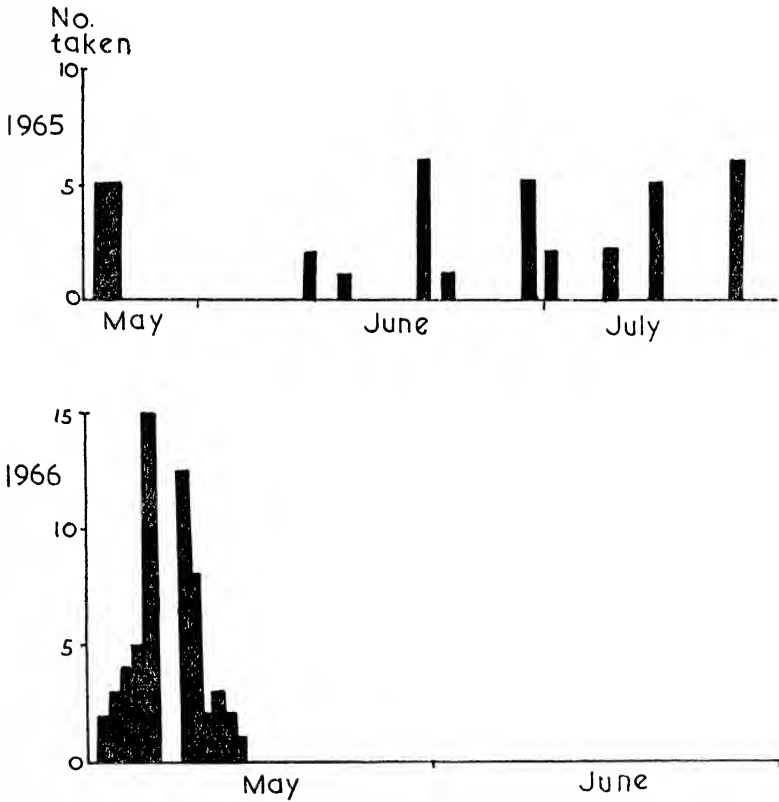


FIGURE 49.—The field captures of adults of *Tetrastichus clavicornis* and *T. pallipes* on Lindow Common, are shown for 1965. The emergence of the adults of these two species is also shown from fruits collected in Kent in the early spring and brought indoors in 1966.

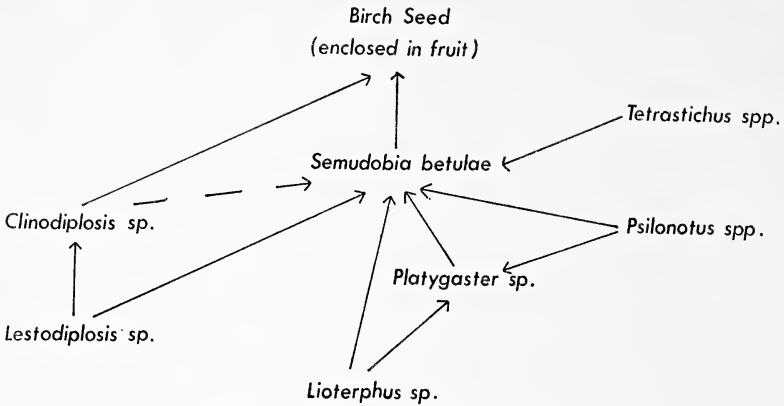


Fig. 50

FIGURE 50.—Food web.

**4. *Pilonotus adamas* Walker and *P. achaeus* Walker
(Chalcidoidea: Pteromalidae)**

These two species of *Pilonotus* are recorded by Peck, Bouček and Hoffer (1964) as living in female birch catkins galled by *Semudobia betulae*. By analogy with allied genera of Pteromalidae (e.g. *Mesopolobus*) it is likely that they are ectoparasites.

Pilonotus has been reared, by the author, from birch catkins collected in 1961, near Scunthorpe in Lincolnshire, and in 1964 from a common not far from Lindow Common, Wilmslow, Cheshire. From the latter material, there were two species of *Pilonotus*, *P. adamas* of which three males and three females were found, and *P. achaeus*, which was represented by one female and three males.

From material collected on birch trees in Bostall Wood, Kent, 10th April 1966, and brought indoors, one male and one female *P. achaeus* emerged on 10th May 1966.

IV. OTHER INSECTS ASSOCIATED WITH FEMALE BIRCH CATKINS

In the field each summer, the female birch catkins are attacked by an unidentified cream-coloured lepidopterous larva. In the summer of 1965, 14% of the catkins were attacked. The larvae eat their way through the catkin, consuming the other inhabitants.

During the winter hibernating insects inside the catkins have been found, and these include Thysanoptera, which according to

Kieffer (1900) feed on Cecidomyiid larvae in some cases; aphids, and a female of the Pteromalid chalcid, *Asaphes vulgaris* Walker. The last named species is a well-known hyperparasite of aphids.

V. DISCUSSION

It is remarkable that a female birch catkin can harbour such a large community of insect species. Although the ten species examined during this survey have the same general habitat, they have mostly quite different feeding habits.

In the family Cecidomyiidae, it is interesting to see how the three species vary morphologically in order to live in their respective places in the female catkin. The larva of *Semudobia betulae* the true gall-maker, is surrounded by food, and is capable only of wriggling movements within the gall, and is generally very inactive. A well-developed sternal spatula is present which is most probably used to prepare a pre-emergence hole for the imago in the woody fruit. No eyespot is present.

On the larva of *Clinodiplosis*, an inquiline feeding on the galled seeds of *S. betulae*, the sternal spatula is less strongly developed, this structure being used to burrow through the soil, at maturity. Well-developed papillae are present on the ventral surface of the body, and there is a dorsal double eyespot. These structures are correlated with movement towards the food source in the female catkin.

On the larva of a predator in the catkin, *Lestodiplosis*, the sternal spatula is absent, but the most striking structures on the body are the pseudopods. A double eyespot is present. *Lestodiplosis* larvae are very active, their extensive movements being attributed to the pseudopods.

Species belonging to the genera *Clinodiplosis* and *Lestodiplosis* need to be revised. Until this is carried out, it will remain unknown whether or not there are only one or two polyphagous species, or a larger number of oligophagous and monophagous species in each genus.

Further work is also needed to establish the nature of the ecological differences between the species of Chalcidoidea which are ectoparasites of *S. betulae*: species of *Lioterphus* and *Psilonotus*. Only *L. pallidicornis* was present at Lindow Common, though both *L. pallidicornis* and *L. fuscicornis* were reared from a collection of galled seeds from Kent. The females of these two species could not be distinguished, though the males are strikingly different.

Concerning *Psilonotus*, both *P. adamas* and *P. achaeus* were reared from catkins from a single locality, and again we have the situation of two closely allied species with apparently the same ecology. The biological differences between them, enabling them to persist together, must be of a rather obscure nature. Perhaps a comparison of the distribution of these chalcids as parasites of *S.*

betulae on the two common species of birch would clarify the situation.

Tetrastichus species differ from the other chalcid parasites in being endophagous. *T. clavicornis* is the main parasitic species of *S. betulae*, while *T. pallipes* was found only occasionally. However, of all the parasites, only *T. pallipes* has been recorded on a host from another plant species (Graham 1960).

The proctotrupoid *Platygaster* is also an endoparasite, but unlike *Tetrastichus*, it attacks the egg of its host.

VI. SUMMARY

1. Three gall midges (Diptera: Cecidomyiidae) and their hymenopterous parasites living in female *Betula* (birch) catkins at Lindow Common, Wilmslow, Cheshire, were studied.
2. *Semudobia betulae* was found to be the only gall-maker, the larva living on the seed inside the cavity of the fruit. Relevant literature, morphology of the stages in the life history, emergence dates of the adults, and the biology are studied.
3. The larva of an inquiline, a *Clinodiplosis* species, found living between the fruits of the female catkin, was seen to feed on the fruits containing galled seeds. Also a *Lestodiplosis* species was found, the larva of which was predatory, living mainly on *Clinodiplosis* larvae, or, in their absence, probably on *S. betulae* and its hymenopterous parasites. The immature stages of these two Cecidomyiids are described, together with their biology.
4. An unidentified *Platygaster* (Hymenoptera: Proctotrupeoidea: Platygasteridae) species was found to be an endoparasite of *S. betulae*. The adult insects emerge at the same time as the host, beginning during the last week in April. Morphology of the stages in the life history together with observations on the biology are given.
5. *Lioterphus pallidicornis* (Hymenoptera: Chalcidoidea: Torymidae) was found to be a frequent ectoparasite of *S. betulae*; less frequently *L. fuscicornis* was also found. Emergence dates of the adult insects and morphology of the immature stages are discussed.
6. *Tetrastichus clavicornis* (Hymenoptera: Chalcidoidea: Eulophidae) was found to be an endoparasite of the larva of *S. betulae*. Occasionally *T. pallipes* was found. Emergence dates for these two species, together with some details of morphology and biology are described.
7. *Pilonotus achaeus* and *Pilonotus adamas* (Hymenoptera: Chalcidoidea: Pteromalidae) were found to be parasitic on *S. betulae*, but were absent from Lindow Common.
8. A predatory lepidopterous larva and other hibernating insects were also found living in female birch catkins.

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